

COMPENSATORY FOLIAGE GROWTH RESPONSE TO PARTIAL
DEFOLIATION IN THE DESERT PERENNIAL SHRUB
ENCELIA FARINOSA (ASTERACEAE)

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ABSTRACT

Seasonal changes of water potential, leaf pubescence and foliage area were compared between two groups of *Encelia farinosa* (brittlebush) growing under field conditions: one group was partial defoliated, the other was left in tact. Partial defoliation at the start of seasonal drought induced compensatory foliage growth with no evidence of ecophysiological compensation, including the expected departure from leaf pubescence values of control plants. The compensatory foliage growth occurred within the first month of drought, but allocation to these additional leaves did not appear to have a pronounced effect on overall plant growth for the season. Leaf pubescence is crucial for maintaining favorable energy and water balance in this species, and it is suggested that the lack of physiological compensation may result from constraints imposed by this character, particularly its important interaction with plant water status during the hot and arid growing season in the Mojave Desert.

Key Words: Drought, leaf pubescence, physiological compensation, foliage area, herbivory.

Productivity for the desert perennial shrub *Encelia farinosa* A. Gray (brittlebush) has been shown to depend on a close coupling between seasonal changes of water availability and leaf morphology (Cunningham and Strain 1969; Odening et al. 1974; Smith and Nobel 1977, 1978; Ehleringer and Mooney 1978; Ehleringer 1988). In particular, lower water potentials that occur during drought cause the production of new leaves with highly reflective leaf pubescence. This pubescence decreases absorption of solar radiation and helps maintain leaf temperatures within a favorable range for photosynthesis while also lowering demand for water used in transpirational cooling (Smith and Nobel 1977; Ehleringer and Mooney 1978; Ehleringer 1983). In the absence of water deficit, or when drought is ameliorated, each new leaf cohort produced develops approximately the same amount of leaf pubescence as the previous leaves rather than becoming more pubescent; however, they do not become less pubescent (Ehleringer 1982). Increasing pubescence during drought is not only beneficial on a short-term physiological basis, it is also associated with longer seasonal activity (Sandquist and Ehleringer 1997).

Although the interrelatedness of leaf pubescence development and plant water status has been extensively examined from a mechanistic standpoint in *E. farinosa*, few studies have explored the ecological factors (other than rainfall) that might affect changing water status and the consequences of these changes, including how such changes interact with constraint or plasticity of the water-relations/leaf-morphology association. For example, the response to partial defoliation, often observed for *E. farinosa*

due to herbivory (especially by rabbits) when availability of other vegetation is scarce (personal observation) or to leaf death caused by short-term freezing temperatures (Bowers 1991; Webb and Bowers 1993; Sandquist and Ehleringer 1996), might lead to lowered water demand owing to a lower transpirational surface area (foliage area; McNaughton 1979). With this, whole plant water status would not be expected to decrease at the same rate as a plant that had not been defoliated. This scenario could lead to a disruption of the usual environmental responses exhibited by *E. farinosa* during drought, especially with regard to leaf pubescence. That is, with improved plant water status leaf pubescence would not develop to the same extent as for an intact plant. Although this result might be beneficial in terms of increased leaf-level photosynthesis through higher light absorption or other physiological compensation, it could be equally detrimental owing to higher, potentially lethal, leaf temperatures, or lower water use efficiency owing to greater transpiration needed to offset higher leaf temperatures. In the latter case the relative loss of water versus carbon gain would be expected to prematurely terminate plant seasonal activity.

Defoliation also begets an imbalance of resource supply and demand between roots and shoots. With severe foliage losses, canopy resource demand becomes lower than the potential root supply. Conversely, root carbohydrate demand significantly outweighs leaf photosynthate supply. This imbalance would likely result in root die-off if there were no compensatory leaf productivity response. One alternative response to leaf defoliation might be increased allocation to new leaves rather than ramp-

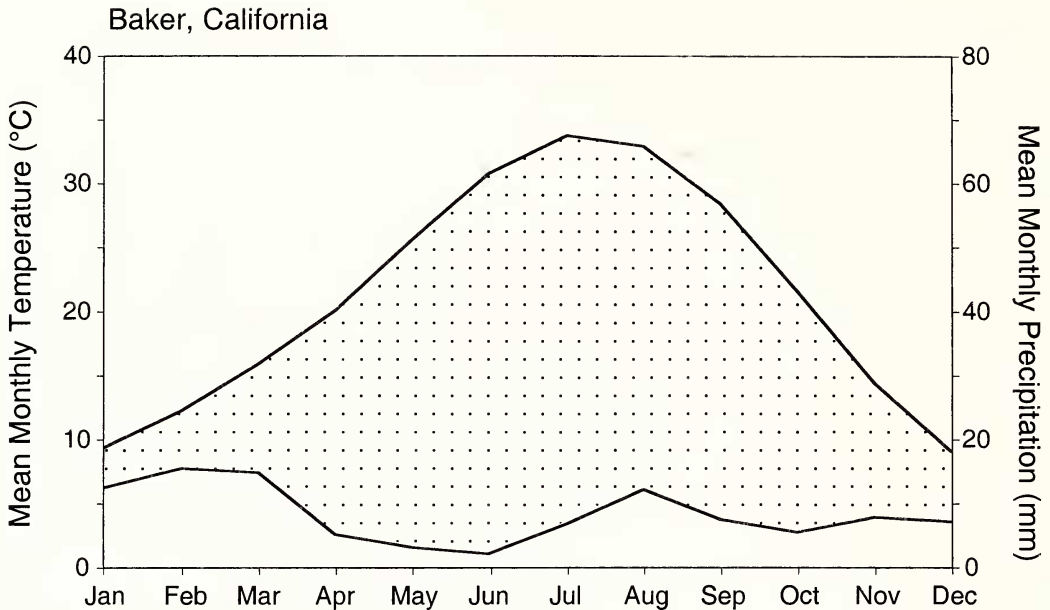


FIG. 1. Climate diagram of monthly mean temperatures (upper line) and precipitation (lower line) for Baker, California (17 km south of study site). Stippled area represents periods of relative drought. Data based on U.S. National Weather Service records for 1972 through 2002.

ing up photosynthesis of existing leaves. In addition to rectifying the imbalance of aboveground vs. belowground supply and demand, this would also re-establish a pattern of water use similar to plants that did not experience defoliation. Such allocation, however, may carry longer-term consequences in terms of reproduction, growth or storage.

In this study it was hypothesized that the reduction of transpiration area (leaves), through defoliation of *E. farinosa*, would lead to either (a) higher plant water status, and subsequently, reduced production of pubescence on new leaves, or (b) compensatory foliage production after defoliation with no changes in leaf pubescence or water status.

Identifying which responses occur owing to defoliation will provide a better understanding of plasticity and constraints associated with foliage growth and leaf pubescence development, and how these responses couple with environmental stresses such as changing water availability and herbivory.

METHODS

Study Site

The field site (35°24'48"N, 116°03'48"W) was located in the Mojave Desert approximately 17 km N of Baker, California at an elevation of 540 m. Mean annual rainfall at Baker, CA is 102 mm, and mean annual temperature is 21.3°C (Fig. 1). The population studied was located on rocky, south-facing slope where *E. farinosa* was the dominant shrub.

Measurements at the field site were made in March, April, June and July of 2001. The first measurements began two weeks after the last rainfall

of spring and ended three days prior to any summer rainfall, thereby encompassing the entire drought season of 2001. Winter and spring rainfall preceding measurements totaled 98 mm, of which 90 mm came between January 8th and March 5th. Plants were in full leaf at the time of first measurements and partial defoliation treatment (25 March).

Partial Defoliation Treatment

From within a population of 72 tagged *E. farinosa* plants, twenty mature plants with full canopies were randomly chosen for partial defoliation treatment. Twenty additional plants were randomly chosen to be controls. On 25 March 2001, after a recent period of high growth, an estimated 50% of all leaves were removed from all stems of the treatment plants. Leaves were removed from the proximal portion of each stem, leaving the upper plant canopy in tact.

Productivity and Physiological Measurement

Foliage area was estimated for all 40 plants on four dates (24 March, 28 April, 6 June and 3 July, 2001) using the following empirically derived formula (Sandquist and Ehleringer 1997),

Foliage area (m²)

$$= \frac{S}{9 \times 10^4} \times \sum_{i=1}^3 \left\{ L_i \times \left[\left(0.106 \times \sum_{j=1}^3 W_{ij} \right) + \left(0.006 \times \sum_{j=1}^3 W_{ij}^2 \right) \right] \right\}$$

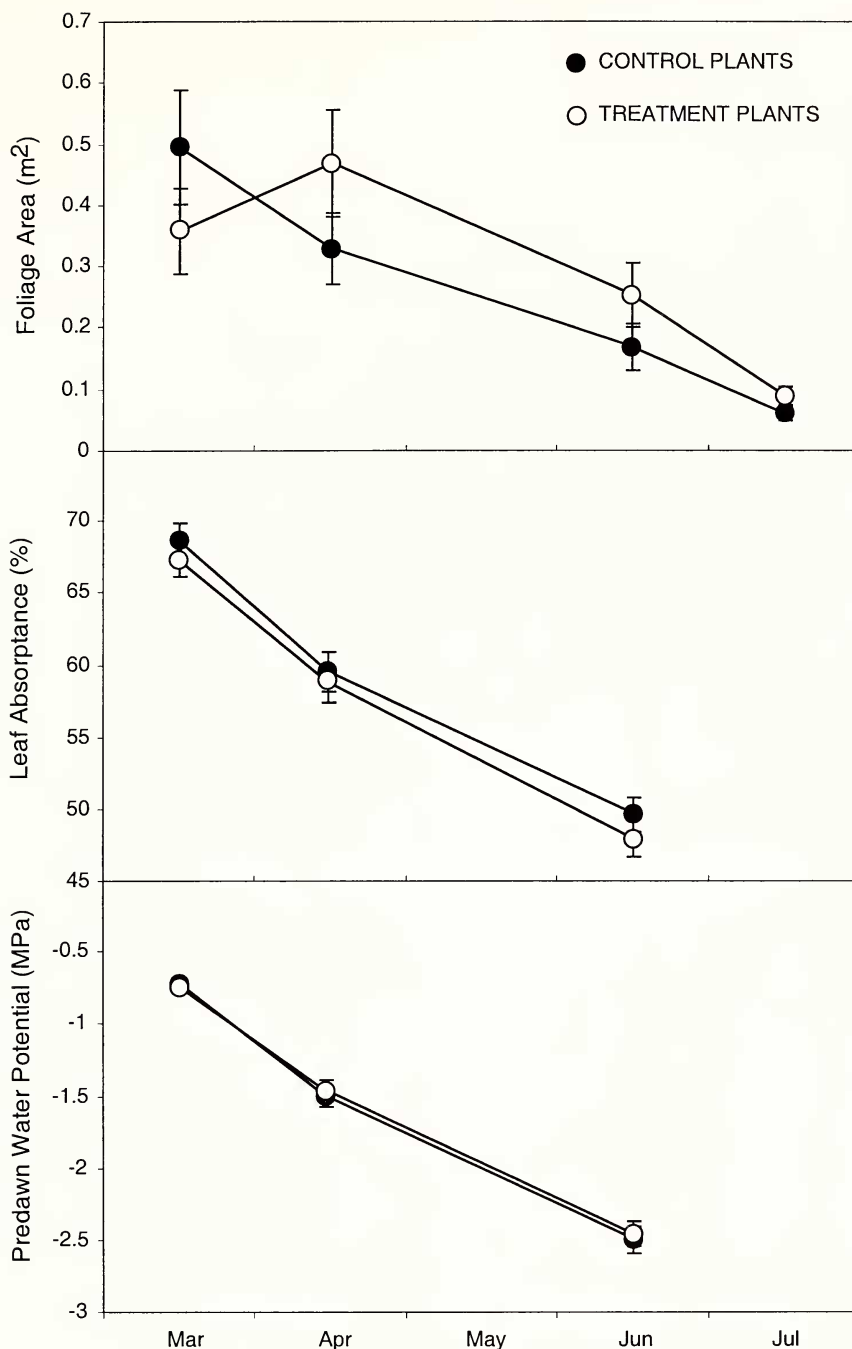


FIG. 2. Seasonal changes of mean predawn water potential, leaf absorptance and foliage area for *Encelia farinosa* control plants (closed symbols) and plants partially defoliated in March (open symbols). N = 20 plants per group. Error bars = 1 standard error.

where S is total number of stems, L_i is number of leaves for stem i , and w_{ij} is leaf width (mm) for leaf j of stem i . Three stems per plant were subjectively chosen to represent the variability of stems sizes on the plant. For each, the total number of leaves (L_i) were counted and leaf widths (w_{ij}) were measured on three leaves that represented the var-

iation of leaf sizes on the stem. The binomial coefficients in the equation (0.106 and 0.006) were empirically determined from a regression of measured leaf widths versus leaf areas on 762 leaves; the intercept was forced through zero ($R^2 = 0.985$; $P < 0.001$). This nondestructive estimate of foliage area compared well with other methods (Sandquist

TABLE 1. MEAN VALUES FOR PERCENT FOLIAGE AREA CHANGE (± 1 SE) OVER THREE TIME PERIODS FOR *ENCELLIA FARINOSA* PARTIALLY DEFOLIATED (TREATMENT) AND CONTROL PLANTS. Significant differences based on ANOVAR were found for Group ($P < 0.001$), Month ($P < 0.001$), Group \times Month ($P = 0.001$) effects.

	% Foliage area change		
	March–April	April–June	June–July
Treatment	+25.5 (7.9)	-48.8 (4.9)	-61.2 (4.2)
Control	-25.0 (6.4)	-54.3 (4.0)	-54.7 (4.3)

1995). To standardize for differences in plant size, foliage area analyses were based on percent foliage area change between months rather than on total foliage area.

Predawn (Ψ_{pd}) and midday (Ψ_{md}) water potential measurements were made 24 March, 28 April and 6 June 2001 using a Scholander-style pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA). On the same dates, three fully expanded leaves of the most recently matured cohort were collected from each plant for determination of leaf absorptance. Leaves were stored in plastic bags with a damp towel and refrigerated until measurements could be made in the laboratory, within 5 d of collection (short-term storage has no effect on leaf absorptance value; Sandquist and Ehleringer 1997).

Leaf absorptance measurements were made within an Ulbricht-type integration sphere in which monochromatic 625 nm light was directed onto the adaxial surface of the leaf. Absorptance is the % of radiation incident on the leaf that is neither reflected nor transmitted. Measurements were made for only the 625 nm wavelength because this wavelength correlates most consistently with leaf absorptance values integrated over the entire energy spectrum (400–3,000 nm) as well as within the photosynthetically active range (400–700 nm; Ehleringer 1981).

Plant canopy volume (m^3) was calculated using the equation for a half spheroid and measurements of plant height, maximum canopy width and width

perpendicular to the maximum width. Measurements were made in March and again in June to determine relative growth over the season.

Statistics

Repeated measures analysis of variance (ANOVAR; JMP 3.1, SAS Institute Inc.) was used to evaluate differences between treatment and control groups for seasonal responses of water potential (pre-dawn and mid-day), leaf absorptance and percent change in foliage area. For all ANOVAR tests the recommendations of Potvin et al. (1990) were used for evaluation of effects due to group, month and group-by-month interaction.

A one-tailed Student's t-test was used to evaluate percent growth (March to June) differences between treatment and control groups. It was hypothesized that treatment plants would grow less than control plants owing to defoliation.

For all analyses, the assumptions of normality and equal variances were met and no transformations of data were necessary.

RESULTS

Treatment plants, after partial defoliation, started with approximately 30% less foliage area than control plants, yet after one month, the foliage area of treatment plants was 40% greater than that of control plants (Fig. 2, Table 1). As a percentage of foliage area change, control plants showed a 25% decrease between March and April whereas treatment plants increased foliage area by 25%. This compensation in leaf area resulted in a significant group effect ($P < 0.001$) and group-by-month interaction ($P = 0.001$; Table 2). The percent change over the following three months was fairly similar between groups (Table 1). By July, foliage area of both groups had converged on a very low level, although treatment plants still maintained about 30% more total foliage area than control plants (Fig. 2).

Between March and June, control plants increased in size by an average of 8.6% (± 6.1 SE), whereas treatment plants actually decreased in size

TABLE 2. SUMMARY OF ANALYSES OF VARIANCE WITH REPEATED MEASURES (F-VALUES AND SIGNIFICANCE LEVELS) FOR TRAITS COMPARED BETWEEN GROUPS (PARTIALLY DEFOLIATED VS. CONTROL) OF *ENCELLIA FARINOSA* OVER FIVE MONTHS IN THE MOJAVE DESERT.

	ANOVAR effects					
	Group		Month		Group \times Month	
	F	P	F	P	F	P
Predawn Water						
Potential (Ψ_{pd})	0.04	0.83 ns	382.5	<0.001***	0.18	0.83 ns
Midday Water						
Potential (Ψ_{md})	0.86	0.36 ns	244.7	<0.001***	2.02	0.15 ns
Leaf Absorptance	0.67	0.41 ns	200.7	<0.001***	0.27	0.75 ns
Percent Foliage						
Change	15.78	<0.001***	54.56	<0.001***	8.27	0.001***

by more than 4.5% (± 7.0 SE). In spite of the high variances for these means, the difference between groups was significant at the $P = 0.08$ level and in the direction predicted.

Predawn water potential showed a significant decline throughout the drought period as would be expected, but there was no significant difference between the treatment and control groups (Fig. 2, Table 2). There was also no significant group \times month effect ($P = 0.83$) thereby indicating that the seasonal decline in predawn water potential was equivalent for both the control and treatment groups (Fig. 2). Similar results were also found for midday water potential (Table 2). Group and group \times month effects were not significant (Table 2), but Ψ_{md} significantly decreased ($P < 0.001$) over the course of the drought: from -1.9 MPa (± 0.05 SE) to -3.4 (± 0.05) for control plants and from -1.7 (± 0.04) to -3.4 (± 0.09) for treatment plants.

Mean leaf absorptance values in March (69% and 67% for control and treatment groups respectively) were in a range that is typically found in the early-to-middle stages of a drought (Sandquist and Ehleringer 1998), suggesting that plants had already experienced some degree of drought stress. However, the seasonal mean absorptance values were not significantly different between the treatment and control groups ($P = 0.42$). As expected, there was a significant decline in leaf absorptance from March to June (Fig. 2, Table 2), and this decline was statistically similar for both treatment and control groups (group \times month effect: $P = 0.75$).

DISCUSSION

Partial defoliation of *Encelia farinosa* plants at the outset of drought was expected to affect the water balance of the plants and thereby influence the absorptance values of leaves produced subsequent to defoliation. Because leaf absorptance couples closely with photosynthetic and energy balance aspects of the leaf (Ehleringer 1988), this predicted compensation (considered physiological compensation) might benefit a defoliated plant because it can occur rapidly and counteract the detriment of productivity loss due of defoliation (McNaughton 1983). However, drawbacks associated with physiological compensation, including greater water loss, might constrain this form of response. Indeed, no physiological compensation was found for the group of treatment plants in this study—those that were partially defoliated at the peak of foliage area production. As compared to control plants, the treatment plants had equivalent leaf absorptance values throughout the post defoliation period (Fig. 2). Compensation came, instead, through an increase in leaf production, after which foliage area of treatment plants actually exceeded that of control plants (Fig. 2). The increase in leaf production not only counterbalanced foliage loss but also resulted in water potential values that were indistinguishable

from control plants throughout the drought period (Fig. 2).

These results suggest that a plastic response of allocation to new foliage growth rather than physiological compensation is favored in *E. farinosa*. This result conflicts with findings for other desert plants, in which physiological compensation was the primary response to defoliation (Detling et al. 1979; Nowak and Caldwell 1984; Senock et al. 1991), but the results are not surprising given that there is a close relationship between energy balance, water loss and leaf morphological features for this species. Indeed, maintenance of higher leaf absorptance (through lower leaf pubescence) as part of the physiological compensation response to defoliation would threaten the temperature balance of the leaf (by absorbing too much radiation) or necessitate increased transpiration, resulting in high water loss relative to carbon gain. On the other hand, foliage compensation, with no relative change in leaf absorptance characteristics, retains the balance of efficient carbon gain vs. water loss without subjecting leaves to potentially lethal radiation absorption. Furthermore, for species in arid environments, where there is a premium on maintaining high root biomass for water uptake, it would be expected that belowground demand for photosynthate would necessitate a response that maximizes photosynthate production with the least water demand.

A number of other studies have also found that partial defoliation rarely results in changes of plant water status (e.g., Nowak and Caldwell 1984; Meinzer and Grantz 1990; Pataki et al. 1998; Hart et al. 2000). These studies suggest or demonstrate that this result stems from increased stomatal conductance and transpiration, but this may not be the case for *E. farinosa* in the current study. Although not tested directly, the absence of water potential differences in this study could plausibly result from compensatory canopy growth rather than leaf-level stomatal compensation.

Surprisingly, the consequences of increased foliage production were only marginally apparent. Treatment plants had only slightly lower total growth over the season than did control plants, and this difference was significant at only the $P = 0.08$ level. While moderate levels of defoliation may not have lasting consequences to the plant, or may even benefit it (McNaughton 1983), the probable consequences of foliage compensation, such as lower reproduction and survival or reduced productivity in subsequent years, were not measured in this study. However, there were no strong immediate costs associated with compensatory foliage growth.

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LITERATURE CITED

- BOWERS, J. E. 1981. Catastrophic freezes in the Sonoran desert. *Desert Plants* 2:232–236.
- CUNNINGHAM, G. L. AND B. R. STRAIN. 1969. An ecological significance of seasonal leaf variability in a desert shrub. *Ecology* 50:400–408.
- DETLING, J. K., M. I. DYER, AND D. T. WINN. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41:127–134.
- EHLERINGER, J. 1981. Leaf absorptances of Mohave and Sonoran desert plants. *Oecologia* 49:366–370.
- . 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *American Journal of Botany* 69:670–675.
- . 1983. Characterization of a glabrate *Encelia farinosa* mutant: morphology, ecophysiology, and field observations. *Oecologia* 57:303–310.
- EHLERINGER, J. R. 1988. Comparative ecophysiology of *Encelia farinosa* and *Encelia frutescens* I. Energy balance considerations. *Oecologia* 76:553–561.
- AND H. A. MOONEY. 1978. Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia* 37:183–200.
- HART, M., E. H. HOGG, AND V. J. LIEFFERS. 2000. Enhanced water relations of residual foliage following defoliation in *Populus tremuloides*. *Canadian Journal of Botany* 78:583–590.
- MCNAUGHTON, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti National Park, Tanzania. *American Naturalist* 113:691–703.
- . 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329–336.
- MEINZER, F. C. AND D. A. GRANTZ. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant, Cell and Environment* 13:383–388.
- NOWAK, R. S. AND M. M. CALDWELL. 1984. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia* 61:311–318.
- ODENING, W. R., B. R. STRAIN, AND W. C. OECHEL. 1974. The effect of decreasing water potential on net CO₂ exchange of intact desert shrubs. *Ecology* 55:1086–1095.
- PATAKI, D. E., R. OREN, AND N. PHILLIPS. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *Journal of Experimental Botany* 49:871–878.
- POTVIN, C., M. J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389–1400.
- SANDQUIST, D. R. 1995. Ecotypic differentiation and physiological adaptability of brittlebush (*Encelia farinosa*) in relationship to environmental diversity. Ph.D. dissertation. University of Utah, Salt Lake City, Utah.
- AND J. R. EHLERINGER. 1996. Potential adaptability and constraints of response to changing climates for *Encelia farinosa* var. *phenicodonta* from southern Baja California, Mexico. *Madroño* 43:465–478.
- AND ———. 1997. Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa* associated with contrasting desert environments. *New Phytologist* 135:635–644.
- AND ———. 1998. Intraspecific variation of drought adaptation in brittlebush: leaf pubescence and timing of leaf loss vary with rainfall. *Oecologia* 113:162–169.
- SENOCK, R. S., W. B. SISSON, AND G. B. DONART. 1991. Compensatory photosynthesis of *Sporobolus flexuosus* (Thurb.) Rydb. following simulated herbivory in the northern Chihuahuan Desert. *Botanical Gazette* 152:275–281.
- SMITH, W. K. AND P. S. NOBEL. 1977. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. *Ecology* 58:1033–1043.
- AND ———. 1978. Influence of irradiation, soil water potential, and leaf temperature on leaf morphology of a desert broadleaf, *Encelia farinosa* Gray (Compositae). *American Journal of Botany* 65:429–432.
- WEBB, R. H. AND J. E. BOWERS. 1993. Changes in frost frequency and desert vegetation assemblages in Grand Canyon, Arizona. Pp. 71–82 in K. T. Redmond and V. L. Tharp (eds.), Proceedings of the ninth annual pacific climate (PACLIM) workshop. California Department of Water Resources, Interagency Ecological Studies Program. Technical report 34.